

deeper blue shade, and is even seen in this aberrant genus as a yellow-green patch. As the immature of the genus *Purpureicephalus* shows the evolution of the mature from a green bird, we have here a case of a structural difference developing at a more rapid rate than a colour-change. We are compelled to indicate our lack of knowledge of how colour-changes and structural changes are produced, but we do know that study of colour and colour-pattern will prove even more valuable than study of structural differences.

EXPLANATION OF PLATE III.

The upper and under sides of the following Parrots:—

1. *Platycercus caledonicus.*
2. " *elegans.*
3. " *flaveolus.*
4. " *adscitus.*
5. " *eximius.*
6. *Purpureicephalus spurius.*
7. *Platycercus icterotis.*
8. " *venustus.*
9. *Barnardius zonarius.*

VII.—*Rejections by Birds of Eggs unlike their own: with Remarks on some of the Cuckoo Problems.* By C. F. M. SWYNNERTON, C.M.B.O.U.

I HAVE referred very briefly to the general result of my first season's experiments in the above connection in 'The Ibis' for October 1916 (p. 557). I returned to the attack last year, partly to ascertain whether really fine discrimination is ever shown. The experiments were interrupted while still incomplete, but Major Meiklejohn's interesting and comprehensive paper in the April 'Ibis,' just received, recalls me to the subject and suggests the publication of my summary of them. Except in the case of the first dozen experiments, I only recorded the details of such as struck me as being of somewhat special interest; but not less, I should say, than fifty were carried out in all

in the two seasons, and this summary of them was written while the later details were still fresh in my mind.

The figures I shall refer to are those of Plate XIX. in 'The Ibis' for October 1916. I hope to figure later some of the actual eggs used.

I have found it very necessary, for convenience and clearness, to coin single word-terms to denote (1) birds that lay only one type of egg (with its variations), and (2) birds that lay two or several distinct types, as do many Cuckoos, Weavers, and Warblers. On the analogy of botanical usage, I am using the adjective "homoic" for the former and "heteroic" for the latter.

RESULTS OF THE EXPERIMENTS.

1. *Acceptances of changeling eggs occurred.*—Among other instances, a Lark-heeled Cuckoo (*Centropus burchelli*), laying pure white dove-like eggs, accepted and sat on a brown Fowl's egg weighing twice as much as one of her own; a *Cisticola natalensis*, with very pale, unspotted, blue eggs, accepted an egg of *Pycnonotus layardi*, again twice as large as her own and coloured like a Tree-Pipit's (cf. fig. 16); a Coly (*C. striatus minor*: fig. 2) accepted and retained a Canary's egg (*Serinus sharpei*) with black spots, and a *Tarsiger stellatus* (Robin-like) a Coly's; and Thick-billed Weavers (*Amblyospiza albifrons*, nearest fig. 14) took back eggs of their own, the appearance of which had been modified by the addition of blotches or smears of brown-madder water-colour paint.

2. *Such acceptance was not necessarily final.*—I placed a Layard Bulbul's egg, of the type shown in fig. 11, in a nest containing two eggs of *Telephonus senegalensis*, removing (as usual) one of the latter (white, with a heavy sepia cap). The Shrike returned, perched on the side of the nest and, leaning over, manipulated one or both of the eggs with her bill, then quietly settled down on to them and sat steadily. On my revisiting the nest later, the Bulbul's egg was gone and the Shrike was sitting on its one egg only. This was the last egg

of its clutch of three, for I had taken one previously, yet, although the eggs were fresh, it continued to incubate it and reared a young bird which gave me some very interesting tongue observations. Very numerous similar instances occurred throughout the experiments, and suggested that we need not regard a Cuckoo's egg found in a nest as quite necessarily finally accepted. The bird's first object seemed usually to be to warm the eggs, and attention to the intruder was postponed.

3. *Nor was the acceptance necessarily always voluntary.*—A Layard's Bulbul with three eggs of the type shown in fig. 16 rejected a Weaver's egg of the type shown in fig. 9 of the same plate. One of the Bulbul's remaining two eggs was then replaced by a pigeon-like egg of *Centropus burchelli*. First one Bulbul returned and perched beside the nest; then its mate arrived and perched on the edge. The first flew off, but the second stood gazing at her new and enormous acquisition, motionless, for approximately one minute. Then she slipped down on to the nest and sat! I waited for a considerable time, and, as she did not stir and it was now getting dark, I left. Next afternoon the nest was pulled down a good deal on one side. The weight of the *Centropus* egg would not have done it alone, as the nest had been firmly placed. That egg was still there, but the Bulbul's egg was gone and a minute search below the tree failed to produce any trace of it. On another occasion a Stonechat (*Pratincola torquata*) adopted a Shrike's egg (*Lanius collaris humeralis*) given her in place of one of her own three. Several days later she was still sitting on it. I now replaced a second of her eggs with another Shrike's egg. When I revisited the nest it was deserted and the Stonechat's egg was gone, the two Shrike's remaining in possession. I am inclined to believe that the Bulbuls and the Stonechats of the above observations, finding the substituted eggs beyond their powers of ejection, accepted it perforce for the time being, and later removed their own egg. The distortion of the Bulbuls' nest may have resulted from a previous effort

to remove the heavy interloper, and in the case of a Warbler (*Cisticola natalensis*) there was suggestive evidence—in the form of a fresh hole made low down in the side of the nest and the position of the “Cuckoo’s” egg in relation to it—of such an attempt previous to the removal of the bird’s own eggs.

4. *Rejection of substitutes.*—The following was a witnessed example. Finding a nest of *Turdus tropicalis*, I replaced one of the Thrush’s three eggs, blue with bold brown spots and blotches, by a Shrike’s (*Lanius humeralis*), whitish closely freckled with light brown. Finding that leaves blocked my view, I shortly returned to the nest to remove them, and the bird flew, as I thought, from it. Taking the incident for an acceptance, therefore, I replaced the Shrike’s egg with that of a Layard’s Bulbul, in which the contrast is even stronger (fig. 16). The bird, on returning, obviously at once noticed it and, leaning over, examined and examined, putting her head down and perhaps turning the egg about; then slipped away. As she did so, her mate appeared, went through the same actions, and left. The female thereupon at once returned, slipped on to the eggs without further hesitation, and sat. I went down and found the Bulbul’s egg gone.

After this discovery I put in a large white egg, brought me by a Kafir and unidentified. The male (brighter bill) came first this time and definitely, from his movements, must have turned the egg about. He looked and looked at it in the gravest manner (a bird *can* look grave!), and at last went off. I feared desertion, if the egg should be beyond their powers of removal, so went over quickly and replaced it with a *small* white egg (*Colius striatus minor*, fig. 2). One of the birds, almost certainly the female, quickly came back, picked the egg up in her bill, and disappeared with it behind the foliage—perhaps wondering at her mate’s difficulty!—then returned and sat on her own two eggs. In a subsequent experiment I watched the Thrushes, again after an inspection by each bird in turn, remove two Shrike’s eggs from the nest; but they flew off behind

the foliage with them, and I again failed to see their final fate. A small boy, who had seen the commencement of the first experiment from a different angle, told me later that the supposed acceptance of the original Shrike's egg was not one, the bird being still a couple of feet from the nest when my approach frightened her away.

In my experiments generally I actually witnessed only a few of the rejections: most of the experiments I had not time to watch, and in those I did watch initial acceptance was the more general rule. In very few cases, again, did I recover the "Cuckoo's" egg. It was evidently usually carried away, as excreta and egg-shells so commonly are, probably to avoid revealing the nest to enemies. In some cases—for all I know, in most—the bird definitely pierced the shell; so that even if the Cuckoo had witnessed the ejection, there would be no possibility of her using the egg again.

5. *Closer selection.*—I placed a specially richly-coloured egg of *Pycnonotus layardi* in the nest of a Yellow-streaked Bulbul (*Phyllastrephus flavistriatus*), removing one of the latter's. Unluckily, the small boy who had showed me the nest at once announced another within a few yards, and I went to inspect. Returning within a very few minutes, I found the Yellow-streaked Bulbuls just drawing off and the Layard Bulbul's egg still in the nest, but *spiked*. The eggs were by no means unlike, excepting for the fact that in the latter the darker markings were less definitely gathered into a zone. I have already mentioned the rejection of an egg of *Sitagra ocellaria* by *Hyphantornis nigriceps* laying spotted blue eggs ('Ibis,' Oct. 1916, pp. 558-9). Though not really like each other, these eggs were not greatly in contrast in a dark nest. But a far better case than either of these was that of a Layard's Bulbul that rejected eggs of its own species that differed very slightly indeed from its own, and even its own egg when its zone was widened by the addition of markings (of the colour and size of the others) in water-colour paint. I will give the whole experiment below. The last

eggs taken from the nest were unluckily destroyed by a cat when I had brought them in to blow. It was a disappointment, as I had hoped to exhibit all, feeling that no one could see them together and deny that selection by foster-parents might have brought about the very closest resemblances that exist between any Cuckoo's eggs and its host's. I hope later to figure the others*.

6. *The ability to distinguish did not depend entirely on the presence of the host's own eggs for comparison, though their presence was undoubtedly helpful.*—When two of the eggs of a Rock-Thrush (*Monticola angolensis*) hatched, a third with which I had been experimenting failed to hatch. I had no other blue eggs in hand, so painted a white egg of *Hyphantornis jamesoni* greenish-blue and substituted it for the Rock-Thrush's egg. It was adopted. A few days later I took it out and put in a Layard Bulbul's egg. It was rejected. I then returned the painted egg, and it was adopted. Two days later I painted it with a number of light brown-madder blotches, and it was rejected. Actually the Weaver's egg was painted of a slightly deeper shade than the Rock-Thrush's and, I fear, rather smearily. It also differed from it in its elongated shape and somewhat smaller size, and it is perhaps doubtful if it would have been accepted had the host's egg been there for comparison. But *wider* departures were at once rejected. A Bulbul (*P. layardi*), that had discriminated very finely, nevertheless accepted two eggs of another form (of her own species) on my finally removing her own two eggs; so that it may actually be that a Cuckoo's best chance would lie in finding a nest with only one egg.

7. *Evidence for the view that polymorphism in the host's eggs may be of use against Cuckoos.*—I watched a Bar-

* On p. 568 of 'The Ibis' for October 1916, I spoke of *Pycnonotus layardi* as laying very variable eggs, but did not include it in the heteroic category. This was hardly correct, for its eggs may be divided into several distinct forms, even though they are close enough to each other and sufficiently connected in some cases by transition to give the superficial appearance of general variability.

throated Warbler (*Apalis thoracica*) accept an egg of *Sitagra ocellaria*. Later I found the egg lying spiked below the nest, and the Warbler sitting. The *Apalis* eggs were white with bold, scanty, red spots, and not far away was another nest of the same species containing blue, closely-freckled eggs just like miniature Stonechats'. I exchanged an egg from each nest. I watched each *Apalis* accept the other's egg; but three hours later the first had rejected, and the egg was lying spiked below the nest. Next day, at noon, the second *Apalis* had not yet rejected; so, regarding it as an acceptance, I removed one of its own eggs for an experiment of another kind. On returning with it six hours later, I found the white, red-spotted egg gone and the bird's own egg in sole possession. Other cases occurred in experiments on Layard's Bulbuls. The very fine discriminators already mentioned rejected an egg of *Lanius humeralis*, accepted their own back, rejected an egg of their own species but of another form, accepted their own back, accepted instead an egg of their own form from another nest, rejected one differing slightly from their own form, accepted their own egg back, rejected the latter on my painting on to it a few additional small markings, widening the zone, rejected an egg of *Colius striatus* substituted for one of their two remaining eggs, did not desert the one survivor, and accepted the other one back. However, on my now substituting, for both these, two eggs belonging to another form, they accepted them, as already related. It was a very pretty experiment.

Weavers (*Hyphantornis jamesoni*: vide figs. 3, 5, 7, 9, 12, 15) very freely and in several experiments rejected eggs of their own species but not their own form.

On the other hand, the pair of Bulbuls (*P. layardi*) that had supplied one of the eggs rejected by the highly discriminating birds—of the form shown in fig. 11—had accepted, instead of it, two other eggs of their own species but belonging to quite different forms.

8. *Some birds accept anything.*—This last-mentioned pair of Bulbuls accepted also, and retained, an egg of *Colius*

striatus minor (fig. 2) and, later, one of *Sitagra ocularia* ('Ibis,' 1908, pl. viii. fig. 5); also, subsequently, a white egg of *Hyphantornis jamesoni* (fig. 3), and, when this was removed by myself, one of *Telephonus senegalus*, white with a heavy sepia cap.

9. *Size and shape not always important where coloration is nearly the same.*—"12.12.15. *Serinus sharpei* nest in low custard-apple bush, conspicuous. Three eggs, fresh. Replaced one (22×15 mm.) with a white egg noticeably smaller than itself (19×16 mm.) and far rounder—*Ispidina natalensis*, practically certainly. Adopted. Later I put in a white *Hyphantornis jamesoni* egg (fig. 3), a good deal bigger than the Canary's egg and differently shaped (26×16 mm.). Adopted. A Layard Bulbul's egg was at once discarded; but the Canary was still sitting on the *Hyphantornis* and smaller egg, and one of its own, a few days later. A Coly (*Colius striatus minor*, fig. 2) with the usual chalky-white eggs (23×18 mm.) accepted and retained one of the Canary's (white, but smooth and of a different shape).

An egg of this Canary is figured in 'The Ibis' for 1908, pl. viii. fig. 4. Those in the nest in question were pure white and hardly spotted at all: one was really unspotted. The small round Kingfisher's egg of the experiment was one of a clutch that I had found in an ant-bear's hole, mixed up with the silt from a heavy rain. The clutch contained a Cuckoo's egg, of the same white colour as the others, but larger (26×20 mm.), and, like the others, it showed slight incubation, indicating that it had been accepted and sat on before the catastrophe occurred. It was probably that of *Coccytes hypopinaris*, a common Cuckoo here; and it is rather a question how its inserter could have got to the Kingfisher's nest, unless this was laid in the main hole or a very shallow passage off it. "Both Millar and the Woodwards have taken the eggs [of this Kingfisher] from the earth of an ant-bear" (Sclater, Fauna S. Africa, iii. p. 84). *Chrysococcyx* has also been recorded as laying in the nest of *Ispidina*, but I am unable to lay hands on the reference.

It is interesting here to recall Mr. Stuart Baker's conviction, arrived at as the result of the study of "very many hundreds" of eggs of Asiatic Cuckoos (including over a thousand of *C. bakeri* alone), that

"2. The majority of foster-parents are totally unconscious of incongruity in size between their own eggs and that of the Cuckoo.

"3. That they are not conscious of variation in shape."
(*Ibis*, 1913, p. 386.)

For "totally unconscious" I would substitute "relatively unsuspecting"; yet I cannot help recalling the great disparity in size that sometimes in butterflies exists between model and mimic, and also various incidents in my insect experiments which showed that a bird may be far more strongly impressed by a very small difference in coloration than by a very large difference in size. My prettiest examples were obtained from a Milanji Bulbul (*Phyllastrephus milanjensis*). *Charaxes ethalion* is a butterfly with black non-mimetic males and many female forms, each of which is a beautiful mimic of one or other of the larger species of *Charaxes* that are protected by their size and power. Yet the Milanji Bulbul, so far from realizing that it was *size* that was at the bottom of her trouble with the larger species, always, after an unpleasant experience with these, refused to touch the small mimetic individuals also, though she readily attacked their differently-coloured males.

10. *Sight, not smell, was the means of recognition.*—In every case in which the coloration of the eggs was the same the substitute was accepted, even by birds that freely rejected eggs of the wrong colour: this even where the eggs belonged to different families and differed in taste (as I ascertained) and therefore, presumably, in smell (which I could not sufficiently appreciate). In my very numerous experiments in regard to the preferences of insectivorous birds the evidence was all against the view that smell is used by them to an appreciable extent for purposes of recognition (though it is true that discomfort was shown

in the presence of highly pungent smells, amounting almost to a volatile discharge, and that short-tongued birds such as Hornbills apparently did their tasting by an intake of breath which, so far, was equivalent to smelling). The view seems to be confirmed further by the acceptance by a Rock-Thrush of a Weaver's egg painted blue, and its rejection of it when a few brown markings were added, the similar rejection by a Bulbul of its own egg when a few small brown markings were added to it, and, if it be supposed that brown-madder paint may smell worse than blue, by the retention of eggs by *Amblyospiza* with much brown-madder paint added. The fact that an egg, drilled but unblown and already smelling unpleasant, was accepted by Bubbles and retained until I removed it two days later, might also be regarded as bearing on the point.

11. *The Cuckoo's habit of removing one of the host's eggs seemed sound.*--In three or four cases I added an egg to a clutch which already contained one accepted egg of the wrong colour. In each case the addition was at once followed by the rejection of one egg. Thus, at a time when the nest of the indiscriminating pair of Layard's Bubbles I have referred to above contained two of the birds' own eggs (fig. 11) and one of *Telephonus senegalus*, I added a fourth egg—a white egg of *Hyphantornis jamesoni* (fig. 3), for which the *Telephonus* egg had been substituted more than twenty hours before—I found shortly afterwards that the *Telephonus* egg had been ejected. As both the Shrike's egg and the Weaver's had previously been adopted, it was probably only the fact that there were now four eggs instead of three that caused the birds to reject one of them—and only one. A Yellow-streaked Bulbul adopted (quite likely, however, only temporarily, for I watched her examine it well) a Coly's egg; but on my putting back her own egg, making three eggs in the nest instead of the original two, she at once on her return flew back to her mate, and one of the birds returned, picked up the Coly's egg in its bill after a good deal of fumbling and trouble, and flew off with it, gradually swerving towards

the ground with (it seemed) the weight of the egg. During the last few yards of her flight she disappeared behind tree-trunks, but I judged that she must have reached the ground about fifty yards from the nest, which was about twenty feet up. A careful search failed to recover the egg, but it had been very visible in the bird's bill as he, or she, flew past within a few feet of myself.

The occasional ejection by the Cuckoo of one of its victim's eggs the day before it inserts its own, quoted by Major Meiklejohn, would seem likely to lessen slightly its chance of getting its own egg accepted; but this is a point yet to be tested. I think that on all the occasions on which I brought the birds' eggs to their original number again after an interval, it was by the return of their own egg. This was never rejected unless its appearance had been altered, and, of course, if the Cuckoo's harmonized well it would not be rejected either.

Against the suggestion conveyed by my results must be placed cases such as that quoted by W. L. Sclater from Ivy ('Fauna S. Africa,' Birds, iii. p. 198). Here a nest of *Andropadus importunus* was found "containing two of the usual eggs . . . in addition to five large Cuckoos' eggs. These all together more than filled the small cup-shaped nest, the rightful occupants of which" had apparently not deserted. Such a case must be rare, and could hardly happen in the case of many foster-parents; but from other records it would seem that this Bulbul is quite the "Hedge-Sparrow" of South Africa, in the sense of being readily duped—a contrast to *Passer arcuatus*, the "Redstart" of the same country. In any case more experiments are needed.

12. *The number of rejections of unmatched eggs so very greatly exceeded the acceptances that conclusions based on the eggs found are likely often to be unreliable, especially if elimination is not well allowed for.*—Without having recorded nearly all my experiments—a pity from this point of view—I should say that rejection of the ill-matched substitutes took place in about 80 per cent. of cases. This

at once suggests an argument which might be urged by critics of the view that mimicry takes place at all in the eggs of heteroic Cuckoos. I have lately had letters from such critics, though they did not use this argument. It is that, for the most part, we see only the successful candidates in each annual "examination." If we could also see the possibility for larger numbers that were "ploughed," we might find that the great majority of the eggs laid in the nests of a given host—even of a host in whose nest we rarely find a wrongly-coloured Cuckoo's egg—by no means resemble its own eggs, and that the alleged tendency to resemble them has no existence till after the "examination."

I once planned an experiment to illustrate this criticism. It was checked at the outset by the general interruption of my experiments, but such as there is of it will just serve my purpose. Taking two Coly eggs (white), I placed each of them in a different Layard Bulbul's nest. From one of these nests four wrongly-coloured eggs had already been ejected, but it still contained an egg of its own species and form that had been adopted. Going the rounds later I found that only one of these Bulbul's nests contained a "Cuckoo's" egg and that this resembled the bird's own.

Conclusion. "A hundred per cent. of the eggs of *Pseudococcyx experimentor* found in the nests of *Pycnonotus layardi* resemble the eggs of the foster-parent." The actual position, in this case, as we happen to know, was that only one egg out of seven placed in the Bulbuls' nests was of this type, the remaining 85 per cent. having been utterly unlike those of the foster-parent. These represented the Cuckoos' eggs that we never see. This definitely limits us, for our direct evidence of mimicry, to eggs seen as soon as inserted and before the foster-parents' return: for, as some of my experiments showed, the latter sometimes remove the offending egg at once—and, by flying away with it, destroy all evidence of its having been there except such as is afforded by the incompleteness of their own clutch. This last line of evidence is fairly useful in Africa, less so in a civilised country in

which one or two eggs might have been removed by some tender-hearted collector.

However, the indirect evidence, which I shall refer to below, seems sufficiently strong.

Other results of our not seeing all the eggs that are rejected would be, I think, to make it difficult always to be sure, except on ovarial evidence and observation of behaviour, (1) of the duration of the laying season of particular birds—it might extend beyond that of the special host, but the eggs then laid would be mostly eliminated before being seen—or (2) of the total number of eggs laid. This is likely, I think, always to be distinctly larger than the number of eggs found by an observer and correctly attributed by him to a particular bird, unless we can assume not merely that the observer has found all the eggs laid but that the Cuckoo will have been successful in matching all her eggs.

DISCUSSION.

1. *Methods of dealing with the Cuckoo's egg.*—I have already shown that the removal of the interloper was the method adopted by nearly all the birds on which I experimented, that it was usually, apparently, carried right away, as are excreta, that it was sometimes spiked and that, in one experiment, it was merely dropped, after spiking, outside the nest. Of the two eggs treated thus, one was probably too heavy for the bird to carry, the other not, and another bird of the same species that was experimented on with a light egg apparently carried it away, for it could not be found. I have already referred to the alternative course, probably followed where the substitute was large. Practically no definite desertion of the bird's own eggs took place, even though some parents were reduced to sitting on a single egg. The Flycatcher, *Bradyornis murinus*, seemed to be an exception, three nests in succession being deserted, eggs and all—in one case after a substitute had been ejected, in the other cases after I had merely visited the nests. In a few cases all the eggs in a nest, substitute and host's eggs, disappeared, and this may have sometimes occurred through

the ejection of the substitute being followed by a decision to remove the eggs from a nest that had been detected; but it did not seem that this occurred in a larger proportion of cases than I found amongst nests on which I did not experiment, and in some cases the damage to the nest suggested that an enemy was responsible. Mr. Stuart Baker has mentioned an instance ('Ibis,' 1913, p. 398) in which all the eggs were smashed, "evidently by a bird's bill"—a case in which it seemed "as if the Shrike, in a fury at the deception attempted on it, had itself broken the Cuckoo's as well as its own eggs." I obtained no such instance myself, and *Lanius humeralis*, on which I experimented several times, was one of the birds that most tended, *apparently*, to remove its eggs after two or three attempts at cuckolding, but Mr. Baker's suggested explanation is quite likely correct. Similarly, the fact that I obtained no instance of desertion of the bird's own egg except in *Bradyornis* does not tell against his supposition that the deserted nests he found containing Cuckoos' eggs were deserted on account of the latter's presence, though this naturally requires a little proof unless such nests were proportionately more numerous than deserted nests of the same species (*Horornis*, *Garrulax*, *Mesia*, *Liothrix*, *Anthus*, *Lanius*, *Surga*, *Cisticola*) not containing Cuckoos' eggs. I remember well that as a school-boy in Ireland and England my main fear, justified by experience, was lest by visiting a nest too frequently or taking too many eggs I might make the bird desert. Here, in Africa, my fear is not so much the desertion of the eggs (though this sometimes occurs) as their disappearance, and the Kafirs, in giving their reason for avoiding tampering with a nest with eggs, or placing a charm in it if they have touched an egg, always say, not that the bird will desert, but that it *will take its eggs away*; cases are sometimes mentioned in which, as in the case I have myself mentioned above, the bird was seen carrying its eggs away. I am inclined to suspect that there really is some difference here, of a general nature, between the birds of the two countries, conceivably in relation to different dominant

classes of enemies. A similar general difference occurs in the number of eggs composing the usual clutch—five in England, three in south-east Africa; and here again the difference is probably dependent on some general difference in the conditions. That desertion is common, at any rate in some species, as a result of the insertion of a Cuckoo's egg, is shown by Major Meiklejohn's quotation of the fact that Wrens (in 150 cases noted by Walter), Willow-Warblers, Wood-Warblers, and Chiffchaffs invariably desert under these circumstances. Another mode of dealing with the Cuckoo's egg would seem to be to cover it with fresh nesting material, so that it remains built into the lining.

2. *The history of the parasitic habit.*—Wallace's view, I think, may be quickly dismissed. It was that, the colours of small birds' eggs being protective—fitting in, as he supposed them to do, with their chequered surroundings of light and shade—a Cuckoo's egg, unlike the others in the nest, would strike a discordant note "and lead to the destruction of the whole set. Those Cuckoos, therefore, which most frequently placed their eggs among the kinds which they resembled, would, in the long run, leave most progeny, and thus the very frequent accord in colour might have been brought about" (Darwinism, 2nd ed. p. 216). I have indicated elsewhere ('Ibis,' Oct. 1916, pp. 531-532)* my view, which must, I think, be shared by field-naturalists generally, that it is impossible to regard Hedge-Sparrows' and Song-Thrushes' eggs, for example, as protectively coloured, and the survival of the "discordant" Cuckoos' eggs accepted by Hedge-Sparrows also tells against the theory. I have stated above that in my experiments, the robbery, probably by enemies, of nests containing discordant eggs was not more frequent than that of nests without them.

Darwin quotes the statement that some Cuckoos "manifest a decided preference for nests containing eggs similar in

* A correspondent regards it as my own view that the Song-Thrush's egg is protectively coloured. Evidently I did not make it sufficiently clear that I was merely stating an illustration of Wallace's theory and that I strongly disagreed with him.

colour to their own"; and I was interested lately, in looking up the 'Origin' for his views on the subject of Cuckoos, to see that the explanation I offered in 'The Ibis' (Oct. 1916, p. 561) for the young Cuckoo's habit of ejection was, in detail, that long ago given by Darwin. I am a bad reader, having little time for it—I have probably not read the 'Origin' through since I was a schoolboy, if then—and the idea came to me independently, as it was likely to do to anyone watching ejection and puzzled over its explanation. I mention the point here merely in order to apologize for having inadvertently brought forward the suggestion as my own.

I was interested further, however, to see that the general theory of the transition to parasitism, as I have seen it given by Newton and others, is also Darwin's. He refers to the fact that various birds occasionally lay their eggs in other birds' nests, quotes the Gallinaceæ rather particularly in this connection, refers to "the singular instinct of the Ostrich," in which family "several hen-birds unite and lay just a few eggs in one nest and then in another, . . . as with the Cuckoo, at intervals of two or three days," and refers to the fact that "the instinct of the American Ostrich, as in the case of *Molothrus bonariensis*, has not as yet been perfected, for a surprising number of eggs lie strewed over the plains, so that in one day's hunting I picked up no less than twenty lost and wasted eggs." Darwin also speaks of the stages in the transition that are illustrated by the American Cow-birds, quoting from Hudson, and especially remarks on the fact that in *M. bonariensis*, with parasitic habits already well developed, "several [birds] together sometimes commence to build an irregular untidy nest of their own," which they apparently never finish, and that "they often lay so many eggs—from fifteen to twenty—in the same foster-nest, that few, if any, can possibly be hatched."

It is possible out of Darwin's material, and with one or two small additional suggestions, to frame the following theory. So far as one can tell at this date, it may represent an approximation to what has actually taken place.

We start with a polygamous species, with several females laying in the same nest, as in *Crotophaga*. The male or first-incubating females drive away late layers or the nest becomes over-full. The layers then go off and either lay in other nests of the same species, not yet full, till the same thing happens there, or, nests failing, drop their eggs about and waste them. In both the earlier and the later nests Darwin's suggested advantage—undelayed incubation of eggs laid at nearly the same date—comes about. Darwin laid stress on this advantage in relation to the Rheas, it being his own theory here, and strongly endorsed the view of "some naturalists" that parasitism on unrelated species would confer a similar advantage; but it may be said, I think, that the advantage would have already been present in the stage thus described—the stage reached by the Rheas,—and that parasitism, therefore, would confer not so much this as a further advantage. For where, instead of wasting their eggs, the layers placed them, nests of their own species being no longer available, in nests of other species (a very natural development), a certain proportion of them would be saved: perhaps a very large proportion when the habit first arose, if it be true that selection has had much to do with the perfecting of the qualities of suspicion and discrimination in hosts, and if overcrowding of the foster-nests were either not serious or were eliminated early by selection. The hens that became broody last, or at least, perhaps through laying most eggs, would tend to be the chief layers in strangers' nests, and the loss of the desire to brood, being now correlated with a habit that brought with it all the advantage between probable survival and certain elimination, might become accentuated in succeeding generations through the action of natural selection.

A point to be borne in mind, I think, is that a primary necessity throughout will have been that of obtaining the right food for the nestling and that the latter may not have been so well adapted at the outset to a somewhat varying diet as it perhaps is now. It may be the case (and this could be tested experimentally and by stomach-examination)

that necessities of diet have much to do with the early stage now represented by the relations between the Cowbirds *Molothrus badius* and *M. rufo-axillaris*, though it is in any case only natural that the first layers in nests of other species should go, where it is available, to a species nearly related to their own.

Again, when the next and bigger step was taken of placing eggs in the nests of quite unrelated birds, food will have remained a prime consideration, and this seems to me to have a bearing on another point. For, surely, the safest rule in this connection, as well as the natural thing to happen, would be for the Cuckoo to base its choice primarily on recognition of the foster-parents that had successfully reared itself. It is quite true that in butterflies, in which recognition is primarily by smell, a male will, after a first pairing, recognize also by sight, as is evidenced by the courtship of model by mimic and mimic by model that I have myself often witnessed. It is similarly possible that, having seen its own egg, a Cuckoo may be influenced by egg-coloration in its choice of nests; but I cannot help feeling that the order of probability, or, if (as is sometimes likely) all three means of recognition are used, the order of importance will be, (1) appearance of foster-parents, (2) of nest, (3) of eggs. The criticism, frankly adduced by Major Meiklejohn himself, that Cuckoos regularly deposit in Hedge-Sparrows' nests eggs unlike those of the foster-parent, seems to me to tell too strongly against the opposite view to be lightly passed over.

Selection would soon follow the adoption of the habit of placing the eggs in other birds' nests—selection of discrimination in the more usual hosts and of deceptive coloration in the Cuckoo's egg. Discrimination may be rarer, and mimicry less needful, at first than later, and it is in this connection that the transition so well illustrated by my experiments is suggestive: the transition between such a bird as the Hedge-Sparrow must be (my experiments on any one species were insufficient to convince me that I

had found an equivalent here) through such species as *Pycnonotus layardi*, individuals of which discriminated closely, others less closely and one or two not at all, to such a species as *Hyphantornis jamesoni*, which, in my experiments, ejected or destroyed all eggs that were appreciably unlike its own. It is even possible that the Hedge-Sparrow may be a recent victim and the Redstart an old one, and the transition between them as much a matter of past selection as of any original difference in discriminating power between the species concerned—not that this will not, in many cases, have existed.

With the growth of discrimination on the part of the species most victimized—and special victimization would be a matter both of abundance and (through natural selection and correct choice of other survivors) of suitable feeding—would come mimicry. I doubt whether this would always end the matter, for, when a Cuckoo's egg became indistinguishable from its host's, variation in the latter would still afford the means of distinguishing it from the Cuckoo's, and it is even imaginable that a race may in some cases have taken place between the host's eggs and those of the overtaking Cuckoo. High distinctiveness might sometimes have been the result. In other cases sheer variability would help much to baffle the Cuckoo whatever its choice were founded on, and useful polymorphism, as in the eggs of the heteroic Warblers and Weavers, might even be selected, and the influence of parasitic birds have thus contributed much, in the course of ages, towards the production of that quality of diversity that to-day so characterizes Passerine eggs. It will not have been the only factor, for the possibility of preference remains, and the actual stimulus to variation will doubtless always have been environmental. Experiments in this last connection might have very interesting results.

The similar diversity that is found in the eggs of Cuckoos has been sufficiently explained by other observers. I am not inclined to regard homoism (if the word is permissible) as necessarily more recent than heteroism in Cuckoos' eggs.

It seems to me rather that the original parasite is likely to have laid eggs of approximately one type, like some of the non-parasitic Cuckoos to-day, and that, whether this was the case or not, the two conditions are likely to have alternated one with the other in any given locality. The homoic condition will have given place to the heteroic where a dominant species, hitherto the chief victim and model for mimicry, has for any reason (including the over-success of the Cuckoo) become relatively scarce, and where it takes several species of birds to make up the population needed for the consequent overflow on the Cuckoo's part. It (the homoic condition) will be resumed again as one of these species becomes abundant and more and more discriminating; for the other types of Cuckoos' eggs, dependent for their continuance on the scarcer or less discriminating hosts, will sooner or later, if the chief host be really abundant, come under its inspection and be eliminated. At the same stroke, obviously, will be eliminated the tendency to choose other species as foster-parents, while instances through difficulty in finding the right foster-parent will also be reduced by the latter's abundance.

In view of the fact that the dominant soft-billed birds are different in different localities and that in some localities there is no very marked dominance in numbers on the part of any favourite species, it is easy to believe that "the eggs of the Cuckoo (*C. canorus*) vary more in colouring and markings than those of any other known species" (Rey's first conclusion, as quoted by Major Meiklejohn). The case is readily comparable with what occurs in mimetic genera in butterflies, such as *Pseudacraea* and *Euralia*. This mention of butterflies at once recalls the fact that in polymorphic mimics the inheritance has been practically proved by breeding experiments to be Mendelian. Further, whether the dominant or the recessive form will be abundant depends on the presence of the appropriate model. The *hippocoon* female form (incomplete recessive) of *Papilio dardanus* is abundant at Chirinda (S. Rhodesia) and also in other places where

its model, *Amauris dominicanus*, is abundant. The *cenea* form (incomplete dominant)* is abundant at Natal, where that *Amauris* model is nearly absent, but *Amauris echeria* abundant. But in each case the scarce form is still kept up in small numbers through the Mendelian relationship and might replace the other form were a change in the numbers of *A. dominicanus* to lead to a corresponding change in the incidence of selection. Other female forms of the species also occur, mostly mimetic, but one or two not mimicking any pattern at present extant amongst models.

The same principles seem likely to apply in the case of the eggs of the Cuckoo. Here we have exactly the same evidence of the dependence of particular forms on the presence of particular models, the same local results from changes in the relative abundance of particular models, the same "mixed" and now non-mimetic forms, scarce or apparently absent where some model dominates completely, more abundant where this is not the case †. And the appearances of the case—the highly distinctive types obviously duly segregated in generation after generation,—the necessities of the case, and the analogy of the butterflies all strongly suggest Mendelian inheritance.

With the criticism of the theory that *similarity of diet* will have produced resemblance between the Cuckoo's egg and the host's, one cannot but agree; but the view that particular foods may affect the coloration of the eggs of birds is not to be summarily dismissed. Dr. Péringuey told me, in 1915, that ducks fed on acorns at the Cape laid black eggs, and I was interested to see a black duck-egg a few days later, shown me by Mr. Fitzsimons of the Port Elizabeth

* This conclusion is indicated by the results, in the F_1 generation, of a series of matings I obtained recently between individuals of a pure *cenea* strain (out of pupæ sent me from Natal by Mr. E. E. Platt) and individuals of pure *hippocoon* parentage from Chirinda.

† The facts here referred to constitute the real evidence for the existence of mimicry in Cuckoos' eggs. Mr. Stuart Baker has stated them very convincingly for the Asiatic Cuckoos in 'The Ibis' for July 1913. The fact that the size of the egg is not reduced where the usual host lays a large egg is also not to be despised.

Museum, and presumably produced in this way. The black deposit was superficial, but in this, of course, it did not differ from the chalk-layer of certain eggs and the heavier blotches of, *e. g.*, certain eggs of *Pycnonotus* and *Phyllastrephus*.

3. *The host's and the Cuckoo's defences.*—The host's defences include, first, means of preventing the Cuckoo from depositing its egg. Attacking or mobbing the Cuckoo is one such means, and here it would seem that the habit of nesting in colonies must be exceedingly useful. I have seen the members of a Weaver colony drive off a Didric Cuckoo, and in a previous instance I saw a similar mobbing, at a large colony, of a dark bird, probably a Cuckoo, that I failed to obtain a sufficiently good view of for identification ('Ibis,' 1908, p. 11). It must be difficult for a Cuckoo to lay undetected in such a colony, and the mobbing is, of course, more formidable than the attack of a single pair of birds. Even so, the Cuckoo hangs about such colonies and is sometimes successful, and, if detection should be avoided—which is unlikely,—the close collection of nests would, of course, improve its opportunity of matching its egg, if it should have become its habit to attempt to do so. Mr. Austin Roberts's observation (Journ. S. A. O. U. ix. 1913, p. 33) that "*Chrysococcyx cupreus* sometimes deposits its eggs in the nest of *Ploceus auricapillus*, but apparently only when there are one or two nests in a tree," has a bearing on this point. As he had spoken of "dozens of nests" in some of the trees, I take his meaning to be that isolated nests are mostly selected. This would seem to testify to the usefulness of the colony.

Prevention failing, the defence afforded by the colouring of the host's own eggs comes into play. I have already ('Ibis,' 1916, pp. 570 & 573; 1917, p. 271) expressed my opinion that, whatever be the correct explanation of variability in such eggs as the Common Guillemot's, polymorphism in the eggs of many small Passerines is probably to be explained as having been selected in relation to the baffling of Cuckoos that might otherwise more often match their eggs. The results of my experiments quoted under Conclusion 7 (p. 132), above, show clearly that there is nothing

visionary about this suggestion, and, in view of my results from the strongly heteroic Warbler, *Apalis thoracica*, I am much interested to note that two eggs of *Chrysococcyx klaasi*, taken by Messrs. Haagner and Ivy from its nests, resembled in coloration (though not in size) the particular form of the Warbler's egg with which they were found (Journ. S. A. O. U. ii. 1906, p. 36, figured pl. iii.).

Discrimination comes next, and this, as my experiments seemed clearly to show, has in some birds probably become a most efficient defence, right up to the point at which the coloration of the Cuckoo's egg exactly resembles that of the host's. The carrying away of the egg that apparently took place in most of my experiments was possibly useful, not merely in relation to detection by enemies, but for the baffling of the Cuckoo, should it be in the habit of ever again utilising the egg, though I do not regard this advantage, if it exists, as other than incidental. Spiking, and the evidences of destruction of the egg seen in Weavers' nests, would be still more effective, but the former may sometimes be merely a convenient way of carrying a large egg out of the nest. This was obviously not the explanation for the spiking of a *Pycnonotus* egg by a *Phyllastrephus*, described above.

Whether its fellow-nestlings, once the Cuckoo is hatched, have any further chance of escape, might be the subject of further observation. Especially might those instances be studied in which the young Cuckoo retains nest-mates. Some nestlings have, from the outset, far greater grasping-power than others and cannot be lifted without bringing the lining of the nest with them. I found that differences in this respect made a difference to the young Cuckoo I experimented on, but I had no really strongly-marked example to test and the Cuckoo successfully solved all reasonable problems that I set him to work on. Against the possibility that grasping-power might be of use to the host's nestling may be set Mr. John Craig's fascinating observations which I have recently seen quoted in Mr. Percival Westell's book on 'British Bird-Life.' Truly Homeric struggles took place

between his two Cuckoos and the prehensile feet were freely used to prevent ejection, but the stronger Cuckoo eventually threw the weaker from the nest, and repeated the performance on its being replaced. Experiments of my own, as well as general observation with regard to Cuckoo nestlings, tell against the view that the hosts ever eject or neglect the latter through noticing the differences between them and their own young, and the probability generally is, I am inclined to think, rather against the explanation of the coloration of the young Koel that I shall refer to below.

The Cuckoo's defence against the attempts to prevent her placing the egg in the nest must, where she does not intimidate, lie largely in cunning and adroitness and in observations of the birds for the purpose of choosing a suitable moment. I am thinking especially of the case of a colony and of those Cuckoos which lay in the nests of Corvidæ, for the problem would be simpler, though not always quite simple, in the case of isolated nests of small birds the eggs of which were not yet being incubated. The thickness and strength of the shell, again, must occasionally save it from breakage when it comes to a scuffle, as well as permitting it to be carried about with impunity. It is even possible that the extraordinarily tough skin of the Honey-guide, selected primarily in another connection, may be highly serviceable to it as a parasite in enabling it to face attacks from heavy Barbets and its other strong victims. Haagner and Ivy (Journ. S. A. O. U. iii. 1907, p. 103) speak of "all the Honey-guides" as "very persistent in 'commandeering' the nest-hole of other birds, as they are generally fiercely attacked by the foster-parents," and the accounts one has read of the actual encounters certainly suggest that they show much fearlessness of their heavier antagonists. Whether the hawk-like appearance of several Cuckoos is backed up by a hawk-like approach to the nest and the insertion of the egg facilitated by the consequent intimidation of the owners is still, I take it, a point for observation. It has been suggested, I believe, that the Drongo-Cuckoos are enabled by their likeness to their hosts to approach the latter's nests

without arousing suspicion. This may actually be so if the theory has been based on observation, but I am impressed by the fact that our African Drongos are more intolerant of the approach of another bird of their own species, not merely to their nest, but even within their "beat," than any other bird I know—and this is saying much.

Once the Cuckoo's egg has been placed in the nest it has to trust to the host's lack of discrimination, or, alternately, to its resemblance to the host's eggs—and to this last its small size is generally acknowledged to contribute. It remains large enough, however, to be likely to give so small a host as a warbler much difficulty in removing it, as I saw in my experiments on *Cisticola*, and one might even amuse oneself by supposing that the *optimum* size might be one not large enough to fill the victim with complete conviction that it was a fraud, yet just sufficiently large to dissuade it, after an attempt or two, from trying to eject it! One of my Grass-Warblers, again *C. natalensis*, accepted and continued to incubate a Layard Bulbul's egg after what appeared to have been an initial attempt to eject it: here the fraud was obvious from the wrong coloration, but the bird had not the enterprise to remove its own eggs on failing with the Bulbul's. It is just conceivable, again—the point could be tested experimentally,—that the thick shell of a Cuckoo's egg, explicable, I believe, as the result of a reduction in size without a corresponding reduction in the amount of lime used, and useful as enabling it to be carried about, may also protect it from being pierced by such weak birds as Warblers—as the Bar-throated Warbler of my experiments pierced thinner-shelled eggs; and that this, with the difficulty of handling it otherwise which must be experienced by such small birds, may account for the Cuckoo's egg being so often left deserted in the nests of Wrens, Willow-Warblers, &c. At the same time, even should it be so strong—which probably it is not,—this would be of no use to it unless its own parent then removed it to another nest. If such intervention *is* the rule in relation to the egg, it seems hard to understand how Walter could have found as many as 150 deserted Cuckoos' eggs in Wrens' nests

alone. At the same time it would be the natural development in response to desertion, and Major Meiklejohn's record of the Hedge-Sparrow's nest, in which the host's eggs were less incubated than the Cuckoo's, does not stand alone. Mr. Ivy records finding a nest of *Andropadus importunus* containing an egg of *Cuculus clamorus*, slightly incubated, and two of the host's, fresh. A still better observation by the same naturalist was one in which a partly incubated egg of *C. solitarius* was placed in a nest which the day before had contained only two fresh *Cossypha caffra* eggs. It seems obvious, therefore, that intervention has to be reckoned with.

After hatching comes the ejection of the fellow-nestlings, and here I might lay stress on two points that have been insufficiently emphasized, I think, in the one or two descriptions I have seen of the process. One is that the young bird is not simply shot out of the nest by an upward heave—the impression that one is, perhaps, given; but that, except in a shallow nest, there is a display of the greatest *will* and *endurance*—Rodin might well take a blind young Cuckoo as the subject for a statue personifying those qualities. Pauses, during which both victim and murderer ask for food and probably, in nature, get it—as they did from me,—punctuated in my experiments what was sometimes a tedious operation, but one during which the young Cuckoo, as I have said elsewhere, did not give back a millimetre of the ground gained until it finally tumbled its victim over the side. Then comes the second point I have referred to. My Cuckoo, at any rate, on bringing about this result, would climb, backwards, right to the top of the nest if he were not there already, and, leaning over or even almost hanging down, would push, and push, and push, into empty air with his back until he was quite certain, apparently, that nothing remained to be pushed. It is to be supposed that the parents would often replace the nestling in the nest if it were found clinging to the outside, otherwise there would be no object in this final *coup-de-grâce*. Then the young Cuckoo would recover itself and climb down again into the nest. The very highly prehensile feet, useful

throughout, were, of course, quite indispensable to the performance of the part of the operation just described. The wings, as Mr. Craig describes, were used largely for steadying the victim on the Cuckoo's back and were very sensitive and useful. The stimulus to the commencement of the operation seemed always to be *movement* on the part of the fellow-nestling.

I have referred above to the coloration of the young Koel. If the explanation given for it in Mr. Pycraft's useful little book, 'The Story of Bird-life,' be the correct one—namely, that it resembles its male parent instead of, as is usual, the mother, because, were it not black, the foster-parents with black young "would promptly kill it on detecting the fraud,"—then it is obvious that some foster-parents continue to discriminate after the egg is hatched. This may be so, and it will be very interesting if it is, but the theory is one that ought to be tested carefully in the field by substitution of wrongly coloured nestlings, or eggs that will produce them, for those of the Crows, &c., that are the Koel's hosts. Possibly it has been so tested.

Finally, we come to the adult Cuckoo, with, in many cases, a close resemblance to some unrelated bird. I have referred to one explanation of these resemblances—that they enable the bird the more easily to insert its egg in its victim's nest. An alternative—or additional—possibility must not, however, be overlooked. It is that, as in most cases of mimicry, the resemblances will be useful in relation to enemies. The Drongo is likely to be a particularly useful model, not merely for its aggressive qualities, but for its nauseating effect on the eater, tested by me so far, however, only on mammals, not hawks. "Nauseousness" seems to me likely to be the model's qualification in nearly all cases of mimicry in birds that have been suggested as models, though "fighting-weight," such as hawks possess, will doubtless also tell. An argument against mimicry generally has been drawn from the extraordinary closeness of the resemblance of *Hierococcyx varius* to *Astur badius* and from the fact that the resemblance extends to the immature plumage.

I will touch on this in dealing, elsewhere, with my experiments on carnivorous animals. Meantime, I may say that it seems to me to tell against mimicry in relation to the host, but not against mimicry for protection from enemies.

Finally, we have the Cuckoo as a possible model for mimicry, suggesting that it, too, sometimes possesses nauseousness. I refer to the resemblance between the females of the Emerald Cuckoo and of *Campophaga nigra* and *hartlaubi*. It even extends to the bunched appearance of the rump, noticeable in the field. I am aware of the objections to the view that these and the other resemblances referred to here are real cases of mimicry and, up to a certain point, share in them myself, but I feel that they are probably strongly protective and that the element of real mimicry in them is probably considerable.

Major Meiklejohn's summary of known fact and of points on which further information is needed is both interesting and likely to be highly useful to investigators. In the one or two places in which the above remarks happen to have overlapped his statement, it has not been done with any idea either of "poaching" or of criticizing—though I think that the view that the Cuckoo bases its choice on egg-coloration requires careful testing. I have merely felt that it is sometimes suggestive to state things from slightly different standpoints. Elsewhere I have tried to suggest one or two additional points for investigation.

VIII.—Obituary.

ALFRED JOHN NORTH.

THE death of Mr. A. J. North, C.M.B.O.U., which took place somewhat suddenly from heart failure on 6 May, 1917, was briefly announced in the October number of 'The Ibis.'

Born on 11 June, 1855, at Melbourne, the second son of Henry and Mary T. North, of Moonee Ponds, Victoria,